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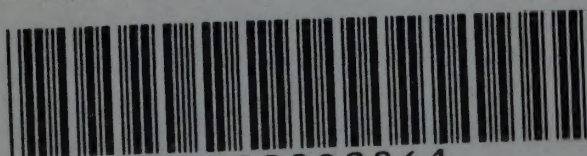
By W. B. CANNON.

[FROM THE LABORATORY OF PHYSIOLOGY IN THE HARVARD MEDICAL SCHOOL.]

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THE NATURE OF GASTRIC PERISTALSIS.¹

By W. B. CANNON.

[From the Laboratory of Physiology in the Harvard Medical School.]

THE characteristic contractile activities of the stomach, so long as gastric digestion persists, are the continuously repeated peristaltic waves running over the pyloric end, and the tonic contraction of the cardiac portion. In many respects the peristaltic waves of the stomach are like the antiperistaltic waves of the colon. Like the waves of the colon they follow one another in a series, without any extensive forerunning inhibition such as is seen in the dog's small intestine. Like those of the colon, also, the waves of the stomach are not abolished by a large dose of nicotine,² which destroys the typical peristalsis of the small intestine.³ Furthermore, since the gastric waves recur with remarkably uniform rhythm, they, like the waves of the colon, must have a pulsating source. The factors explaining colonic antiperistalsis may be expected, therefore, to account for the gastric waves as well.

THE RELATIONS OF GASTRIC TONUS, INTRAGASTRIC PRESSURE, AND PERISTALSIS.

As the condition for the appearance of colonic antiperistalsis an important relation has been found to exist between the internal pressure and the tonic state of the neuromusculature.⁴ In the stomach

¹ A preliminary account of this investigation was presented at the meeting of the American Physiological Society, December, 1910. See Proceedings, This journal, 1911, xxvii, p. xii.

² CANNON: This journal, 1909, xxiii, p. xxvii.

³ BAYLISS and STARLING: Journal of physiology, 1899, xxiv, p. 115.

⁴ CANNON: This journal, 1911, xxix, p. 241.

also the same factors are operative, as can be demonstrated in various ways.

1. If a cat which has not recently taken food is etherized, its spinal cord destroyed below the brachial region, and its stomach exposed by opening the abdomen under warm normal salt solution, the stomach may be found moderately contracted (*i. e.*, in a tonic state), or relaxed and flaccid. In either case the organ will be inactive. If now fluid is introduced into the stomach, the effect will differ according to the status of the muscle. In the contracted stomach the introduced fluid encounters resistance, the pressure applied causes distention of the gastric walls, and peristaltic waves are at once started. In the relaxed stomach, on the other hand, the introduction of even large amounts of fluid usually has no effect — the walls simply retreat before the increasing content.

These observations show that tonus (*i. e.*, a shortened state) may be present in muscle without observable activity, that extension of atonic muscle does not produce activity, but that extension of tonic muscle results in the characteristic rhythm.

That distention of the stomach is a stimulus to its contractions has long been observed. Spallanzani noted that when a hen, starved for a day, was given nuts to eat, no movements of the stomach occurred so long as the organ contained only a few nuts, but that activity started promptly as soon as the stomach began to be full.⁵ Hofmeister and Schütz have recorded the appearance of powerful contractions of the excised stomach of the dog when it was inflated with air and carbon dioxide.⁶ And Ducceschi found that distention of the gastric walls caused the appearance of rhythmic contractions, and that within limits the amplitude of these contractions increased progressively as distention increased.⁷ All these observations are in accord with results obtained by experimentally stretching the smooth muscle of various other hollow viscera.⁸ In none of these instances, however, so far as I have been able to learn, was any attention paid

⁵ SPALLANZANI: *Versuche über das Verdauungs-Geschäfte*, translated from the Italian, Leipzig, 1785, p. 30.

⁶ HOFMEISTER and SCHÜTZ: *Archiv für experimentelle Pathologie und Pharmakologie*, 1885, xx, p. 15.

⁷ DUCCESCHI: *Archivio per le scienze mediche*, 1897, xxi, pp. 146, 149.

⁸ See CANNON: *This journal*, 1911, xxix, p 240.

to the condition of the neuromusculature when the stretching was performed. The point which I wish to emphasize is that the tension may be regarded as composed of two factors, the tonic state of the muscle and the internal pressure. Only when the muscle is shortened and resilient, *i. e.*, in a state of tonus, does distention or stretching, in my experience, result in contraction. The muscle, in other words, must first of all be in a condition to be *stretched* and not merely unresistingly elongated, before stretching can be properly regarded as the efficient stimulus for rhythmic contractions.

2. A second consideration indicating the importance of the tonic state for rhythmic activity is that during gastric digestion the stomach maintains its contractions with a considerable tonic tightening always existent. Many observers have recorded the pressures which prevail in the stomach during its activity — pressures which vary between 6 and 19 cm. of water in the cardiac end.⁹ These persistent pressures measure the degree of tonus of the gastric muscle. The tension which is the favoring state for rhythmic activity is provided in the neuromusculature itself. The condition of the gastric wall while peristaltic waves are running is, therefore, as if the wall had been stretched by the contents.

3. Still further evidence of the importance of tonic contraction for rhythmic activity of the stomach is found in the observation that tonic and rhythmic contraction vary concomitantly in experimental conditions. (a) Stimulation of the vagus nerve is known to increase markedly the tonus of gastric muscle, and, with that, to augment the peristaltic contractions.¹⁰ (b) Severance of the vagus nerves causes a temporary loss of tonus of œsophageal and gastric smooth muscle and, with that, an absence or marked weakness of peristalsis.¹¹ (c) Administering a small dose of adrenalin (1 : 10,000) abolishes intragastric pressure (which measures the muscular tonus); and simultaneously peristalsis ceases. Fig. 1 is a record of intragastric pressure

⁹ See V. PFUNGEN : *Centralblatt für Physiologie*, 1887, i, pp. 220, 275; MORITZ: *Zeitschrift für Biologie*, 1895, xxxii, pp. 356-358; SICK: *Deutsches Archiv für klinische Medizin*, 1906, lxxxviii, p. 190.

¹⁰ See MAY, *Journal of physiology*, 1904, xxxi, p. 264; also protocol, p. 255, *infra*.

¹¹ CANNON: *This journal*, 1906, xvii, pp. 431, 432; 1907, xix, p. 441; DUCESCHI: *Archivio di fisiologia*, 1910, viii, p. 586.

(lower curve), obtained by introducing a tube through the œsophagus into an active stomach filled with fluid, and of gastric peristalsis (upper curve), registered by means of a thread connecting the pyloric portion of the stomach with a writing lever. The animal had been etherized, its lower spinal cord pithed, and its abdomen opened under warm normal salt solution. As the record shows, peristaltic waves

were not restored to the pyloric end of the stomach until nearly forty-five seconds after the pressure (the tonus) began to rise. (d) Artificial establishment of tonus in an excised stomach causes the appearance of peristalsis. A cat was etherized, the aorta severed, and the bloodless stomach removed. The stomach, tied at the pylorus, was slightly distended with warm 0.2 per cent hydro-

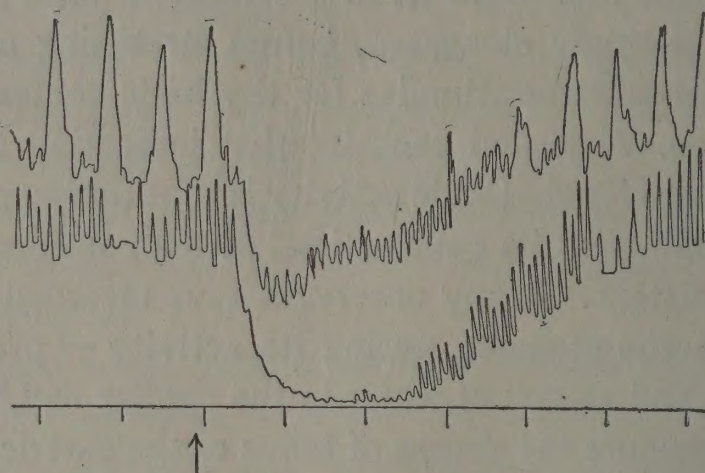


FIGURE 1.—Records of intragastric pressure and peristalsis of the pyloric end of the stomach. Peristalsis (upper curve) begins after pressure (lower curve) has begun to rise. Time, half-minutes.

chloric acid, then tied at the cardia, and placed in a small dish containing 500 c.c. of warm oxygenated Ringer's solution. No change occurred. Now 2.5 c.c. of a 10 per cent solution of barium chloride, which causes tonic contraction of smooth muscle, were poured into the Ringer's solution. As the excised stomach became contracted, peristaltic waves began to pass towards the pylorus. Fig. 2 is a photograph of these waves. In one instance they continued thus with regularity for nearly a half-hour. The concomitant variation of tonic contraction and rhythmic activity in all these instances clearly indicates a causal relation between the two phenomena.

All the evidence thus far adduced — (1) that distention of the inactive stomach causes contraction only when the muscle is tonically shortened, (2) that while the stomach is normally active a considerable intragastric pressure prevails (*i. e.*, the muscle is in sustained tension), and (3) that gastric peristalsis is augmented or weakened, is caused to appear or disappear, as the tension on the contents is increased or decreased — all this evidence points to two factors

underlying rhythmic peristalsis of the stomach, the tonic state of the neuromusculature, and internal pressure which holds that neuromusculature in tension. As foregoing evidence has shown, the tension can be produced in two ways: by increasing the gastric contents and thus stretching the shortened musculature, or by such stimulation of the musculature that it is made to press tonically upon the contents. In the former case the two factors are separable; the musculature may exist in the shortened state without notable tension, and be put on a stretch only when internal pressure is applied. In the latter case the states of tonus and of internal pressure would be developed simultaneously. Now with tonus and internal pressure given as the elements for peristaltic activity, how can the peculiar manifestations of that activity in the stomach be explained?

THE SHAPE OF THE STOMACH AND THE PULSATING SOURCE OF PERISTALTIC WAVES.

There is evidence that the shape of the stomach is a primary factor in determining certain characteristics of gastric peristalsis. The stomach when first filled is roughly conical, — large in circumference at the cardiac end and progressively smaller as the pylorus is approached (see Fig. 2). If the contents are fluid or semifluid, and are subjected to the tension of the gastric musculature, the pressure throughout the contents (gravity aside) will be uniform. Every unit area of the wall will then be supporting the same pressure. Obviously a circumference of given width in the larger cardiac end will be subjected to greater total stress than a circumference of equal width in the smaller pyloric end. Since the forces in the inactive stomach are in equilibrium, however, the circular muscle of the cardiac end necessarily has to exert stronger tension than that in the pyloric end. And furthermore, since the muscular wall of the cardiac portion is thinner than that of the pyloric end, there are fewer muscle fibres in equal cross-sections. The greater circumference and the weaker musculature both tend to place the cardiac region at a disadvantage.

In a previous paper I have pointed out that it is difficult to define the exact relation between the degree of tonus and the internal pressure, which results in effective rhythmic contraction. The internal pressure may be too slight to evoke a response in the tonically con-

tracted muscle, or it may be too great.¹² Ducceschi's observation that by causing intragastric pressure he could first rouse the inactive muscle into activity and that then by gradually increasing the pressure he could produce, after a maximum rhythmic response, an abolition of activity,¹³ is in harmony with my observations on the colon. There is then possible a subliminal, an optimum and a supermaximal internal pressure for stimulating contractile response. On the basis of these observations we may assume that at first the muscles of the cardiac end are too much distended to respond, and that those of the pyloric end are too little distended. Between the large cardiac end and the small pyloric end, however, along the conically shaped organ, the relations of internal pressure and tonus will be intermediate. At some circumference in this region the relations will be such that the neuromusculature will respond by contraction. This circumference will be the first seat of the rhythmic pulsations which start the peristaltic waves.

Experimental support for the foregoing reasoning was secured by noting the effect on gastric peristalsis as intragastric pressure was increased and decreased.

A cat not fed for thirty-six hours, was etherized and given subcutaneously 1 c.c. of 1 per cent morphine sulphate; its spinal cord was pithed below the brachial region, and the abdomen opened under warm normal salt solution. At 11.25, 0.5 per cent HCl was introduced through a tube reaching through the œsophagus to the stomach. The empty stomach was slightly distended, but no peristalsis occurred. At 11.28, the cardiac end of the stomach was lifted out of the salt solution and quickly brushed with a 5 per cent BaCl₂ solution. At 11.32, shallow peristaltic waves began to pass over the stomach. In the interval, 11.34-39, more weak HCl was

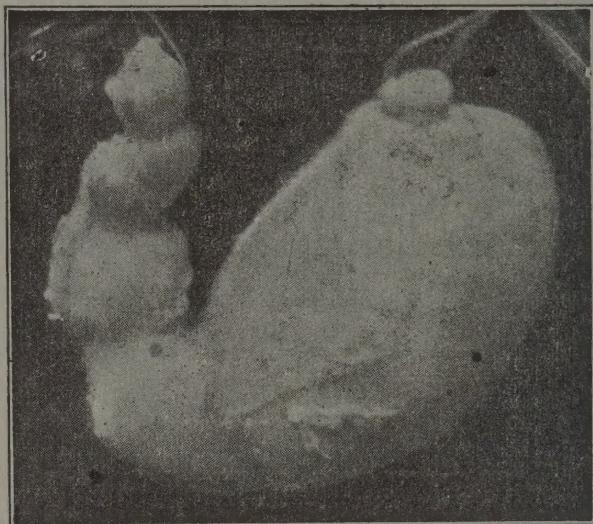


FIGURE 2. — Photograph of excised stomach in which peristaltic waves started when the stomach was tonically contracted by barium chloride.

¹² CANNON: This journal, 1911, xxix, p. 247.

¹³ DUCCESCHI: Archivio per le scienze mediche, 1897, xxi, p. 147.

introduced and the waves disappeared, then about 30 c.c. withdrawn and they reappeared, again 30 c.c. introduced and they disappeared, 40 c.c. now withdrawn and waves, deeper than before, appeared; more HCl withdrawn until walls began to collapse, the waves disappeared. After the stomach was emptied, at 11.43, 50 c.c. of the 0.5 per cent HCl was introduced at 11.45, without starting peristalsis. At 11.48, 10 c.c. withdrawn, whereupon waves started at the pyloric end. Between 11.50 and 11.54, 40 c.c. were added to the contents very gradually, with the result that peristalsis was continued, but only at the end of the antrum. At 11.55, 45 c.c. withdrawn; peristalsis now began on the cardiac end and passed to the pylorus. At 12.05, manometer connected with the œsophageal tube, 20 c.c. introduced, pressure between 2.5 and 3.5 cm., peristalsis on pyloric end. At 12.10, 10 c.c. removed, no change, then 10 c.c. more removed, peristalsis started nearer cardiac end — pressure between 1.5 and 2.5. At 12.15, 40 c.c. introduced, peristalsis driven to end of antrum. Now the right vagus was stimulated, the stomach was strongly contracted especially in the pyloric end, and intragastric pressure rose above 22 cm. The pressure fell to 5–7 cm., and peristalsis, starting near the cardiac end, continued for nearly fifteen minutes. At 12.33, no peristalsis, pressure between 2 and 3 cm. At 12.35, 10 c.c. removed, pressure 1.5–2 cm., peristalsis reappeared. At 12.40, 100 c.c. introduced, peristalsis disappeared; right vagus stimulated, pressure rose to over 21 cm., then sank to 5–7 cm., peristalsis began near cardiac end and ran deep over antrum.

As the foregoing protocol and as other similar observations on the active exposed and on the active isolated stomach show, when intragastric pressure is increased without change in the state of the musculature, the place of origin of the waves is shifted towards the pylorus. And when the pressure is decreased by withdrawing some of the contents the place of origin is shifted towards the fundus. By the former procedure the over-stretched region (at the cardiac end) is extended, and the contracting circumference, having to meet a greater distending force, is moved to a region where the muscles are stronger and in a smaller ring. By the latter procedure precisely the opposite condition is brought about, — the muscle-rings towards the cardiac end, gradually less stretched beyond their responding power, begin to contract, and in consequence the source of the waves is moved farther towards the area of weakest musculature and largest circumference.

When the relation of tonus and internal pressure is such that contraction is stimulated, the contracting muscle-ring is, during the

phase of shortening, refractory to stimulation. The refractory phase of smooth muscle with its local nervous system was indeed first demonstrated in the stomach.¹⁴ The contracting muscle-ring displaces material, which is probably accommodated in the cardiac end where the weakest muscles are working against greatest obstacles. As the contracted circumference relaxes, however, the tonic pressure from the cardiac end again stretches the ring. Thus the contractions would be repeated rhythmically at this point, for the same reasons that have been given for the rhythmic response of the tonic ring in the colon.¹⁵ The pulsatile action of the source of gastric peristaltic waves is indicated by the larger oscillations in the pressure curve of Fig. 1. The waves once started move onward continuously; their starting point, however, by its rhythmic contraction, rhythmically increases intragastric pressure.

THE TRANSMISSION OF THE PERISTALTIC WAVES.

The passage of peristaltic waves away from the pulsatile source must next be considered. These waves normally move only towards the pylorus. This direction is not taken, however, because the neuromusculature acts only in that direction. Again like the colon, the stomach may exhibit both peristalsis and anti-peristalsis. I have previously reported that a tonus ring made by applying barium chloride solution near the pylorus of a cat's stomach, will reverse the peristaltic waves over the antrum, and that excised frog's stomach, distended with normal salt solution, will show peristaltic or antiperistaltic waves according to which end of the organ is set in tonic constriction.¹⁶ The failure of peristalsis to move from the pulsating source in the normal stomach backwards over the cardiac end is due, on the basis of the above reasoning, solely to the stretching of the musculature of that region beyond its ability to respond. Indeed, if it were not so stretched, it would itself be the pulsating source. In other words, the source is as near the fundus as the relation between tonus and internal pressure will permit; towards the fundus from that circumference the over-stretched muscle exerts merely a tonic grasp

¹⁴ See DUCCESCHI: *Archivio per le scienze mediche*, 1897, xxi, pp. 165, 166.

¹⁵ See CANNON: *This journal*, 1911, xxix, p. 243.

¹⁶ CANNON: *This journal*, 1909, xxiii, p. xxvii.

on the contents; towards the pylorus the muscle, not over-stretched, is capable of being roused to contraction.

The question as to how the contraction wave moves onward from its source is the same for the stomach as for the colon. The wave might progress as the result of an advancing ring of internal change, or it might progress because a ring of contraction would increase internal pressure on contiguous rings and thus call them into activity. In either case the rings just relaxing would be less irritable than rings already relaxed, and the effect, therefore, must be a wave moving steadily in one direction.¹⁷

Evidence as to which of the foregoing methods of transmission of the contraction wave prevails in the stomach was obtained by making, with aseptic precautions, incisions reaching to the submucous connective tissue and encircling the stomach. The myenteric plexus was thus completely severed. In different animals one, two, four, and six such complete interruptions were produced. When the animals had recovered from the operation (in all cases within four weeks), they were fed, and, after gastric digestion was well started, the stomach was exposed in the manner already described. Thus the movement of the peristaltic waves could be directly watched.

The trough of the wave was the part most easily followed, and its course could be observed best in stomachs with only one or two encircling incisions. In these cases waves at times passed over the organ as if no cut had been made. At other times there was only a slight hesitation at the ring of incision. Again, contraction occurred on the pyloric side of the cut and a wave started away just before the approaching wave arrived; the approaching wave then ended at the cut. Occasionally waves began at the cut without any perceptible waves appearing above it. In the case in which six rings of incision were made, peristaltic waves were clearly seen passing in monotonous rhythm over fully three-fourths of the stomach, without any disorganization, and with only occasional slight retardations at one or another of the rings.

Magnus has shown that the movements and the reflex of the small intestine persist after the mucosa and submucosa have been removed.¹⁸ The submucous plexus, therefore, is probably not concerned in the

¹⁷ See CANNON: This journal, 1911, xxix, p. 245.

¹⁸ MAGNUS: Archiv für die gesammte Physiologie, 1904, cii, p. 349.

motor functions of the canal. In the above experiments the continuity of the myenteric plexus was so far broken as to render it incapable of conducting. That peristaltic waves nevertheless can move with normal regularity over the stomach indicates that conduction by internal change (*i. e.*, the progress of a state of excitation in the nerve net), is not a necessary conclusion from the observed facts.

A supposition accounting for the results obtained in the above experiments and in harmony with previous considerations is as follows. A contraction of the pulsating ring increases the pressure in the stomach. The increased pressure does not affect the contiguous muscle towards the fundus except to stretch it still more beyond its responding power. The muscle towards the pylorus, however, only contracts as internal pressure is increased. The rise of internal pressure resulting from a pulsation would therefore cause the contiguous muscle to be stretched and it would respond by contraction. Its contraction would in turn affect in the same manner the area lying immediately beyond, and thus the contraction would progress as a wave. It could not return on its path because, as already explained in relation to colonic antiperistalsis, the contraction wave trails behind itself an area of lessened irritability.¹⁹ Thus severance of the myenteric plexus might have very little effect on peristalsis, for a wave approaching a ring of incision would distend the region beyond the ring quite as readily as under normal conditions, and the usual results would follow.

The foregoing explanation would require the pressure in the stomach to be greater as the pylorus is approached. Observations of intragastric pressure in different parts of the stomach show that such is the fact. In v. Pfungen's case of gastric fistula he found the pressure in the cardiac end 19 cm. of water, and that directly in front of the pylorus 162 cm. Moritz's records for the cardiac end varied between 6 and 8 cm., while in the pyloric end pressures rising to 38, 40, and even 60 cm. of water were obtained, with a usual range between 20 and 30 cm. Sick, using Moritz's method, found between 7 and 16 cm. of pressure in the cardiac end, contrasted with pressures from 25 to 42 cm. in the pyloric end.²⁰ These greater pressures in the pyloric end are doubtless due to the fact that the peristaltic waves become grad-

¹⁹ CANNON: This journal, 1911, xxix, p. 246.

²⁰ See v. PFUNGEN, and MORITZ, and SICK: *Loc. cit.*

ually deeper as the pyloric portion becomes gradually narrower. The contraction is increased, therefore, as the waves move into areas of thicker musculature contracting in smaller circumference. The greater mechanical stimulus required to induce contraction in this region compared with the cardiac region under the same conditions of tonus is provided naturally in the more powerful response of the stronger muscle. Thus, concomitantly, increased internal pressure (needed to stimulate contraction) and increased contraction (resulting in greater pressure) interact with and augment each other, as the waves move towards the pylorus.

CONDITIONS WHEN THE MID-REGION BECOMES TUBULAR.

In 1898, I showed that as the stomach empties the mid-region becomes gradually narrowed into a tubular portion.²¹ The waves then originate at the upper end of this gastric tube at a tonic ring separating the tube from the rounded cardiac sac. The ring forms a depression which has been repeatedly noted in X-ray photographs of the human stomach,²² and is observable also in the exposed stomach of lower animals. This persistent constriction has been called the "incisura cardiaca." The activity of this deepened ring can best be understood in terms of the activity of the tonic ring in the colon. As the protocol (p. 255) records, and as numerous other cases have proved, the inactive stomach can be made to manifest peristalsis by producing with barium chloride a tonic ring in the cardiac end or in a circumference near the middle of the stomach. Since the stomach when first filled has a conical shape, the change to a tubular form in the mid-region involves greater contraction at the cardiac end than at the pyloric end (see Fig. 3). Because the cardiac incisure, at the extreme cardiac end of the tube, is therefore more contracted than any other part of the stomach, it, like the tonus ring in the colon, is probably more easily distended than any other part.²³ Distention by internal

²¹ CANNON: This journal, 1898, i, p. 371.

²² See KAESTLE, RIEDER, and ROSENTHAL: Archives of the Röntgen ray, 1910, xv, pp. 21-24.

²³ The condition presented by the cardiac incisure clearly indicates the distinction to be drawn between muscle in a small ring (as in the antrum), and a small ring of tonically contracted muscle.

pressure, however, causes the ring to respond rhythmically. Each contraction sends off a wave towards the pylorus, and as the food is forced on into the intestine, the cardiac sac, by tonically pressing on its contents, provides more material for the waves, while helping to maintain the internal pressure required for the continuance of peristalsis. Only after the medium for distributing internal pressure — *i. e.*, the contents — has disappeared, does peristalsis normally cease.

ORIGIN AND MAINTENANCE OF GASTRIC TONUS.

The important rôle of muscular tonus, developed in the foregoing discussion as a fundamental condition for gastric peristalsis, gives new meaning to vagus functions in the stomach. Vagus stimulation, as is well known, causes, after a momentary inhibition, a marked increase of tonus of the gastric muscle (see protocol, p. 256). With brief stimulation subsidence to the previous state may be rapid, but when a vagus nerve is repeatedly stimulated, the tonus increases more permanently after each stimulation, and in some instances may remain continuously high.²⁴ On the other hand, when both nerves are severed, the first effect is often total absence of activity.²⁵ Because peristalsis is associated with an augmentation of gastric tonus when a vagus nerve is stimulated, these nerves have been called the "motor nerves" of the stomach. From foregoing evidence, however, we may conclude that the function of the vagi is solely to set the gastric muscles in a tonic state, to make them exert a tension, so that they are as if stretched by the contents; and that the result of this condition is peristalsis.

The prime importance of the tonic state for the appearance of peristalsis is emphasized by development of a remarkable tonic state after the stomach is isolated from the central nervous system. As

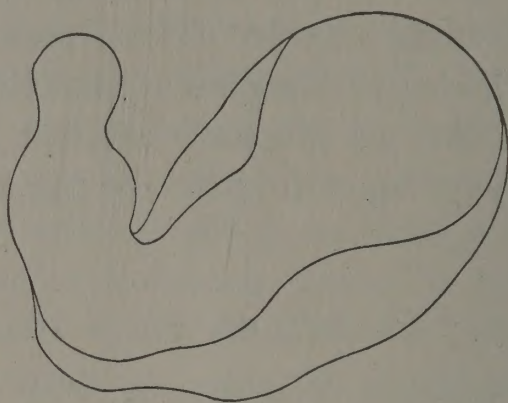


FIGURE 3. — Diagram showing that the change from the conical to the tubular shape of the stomach requires greater contraction at the cardiac end of the tube.

²⁴ MAY: *Loc. cit.*, pp. 262, 264.

²⁵ CANNON: This journal, 1906, xvii, p. 431.

I pointed out in 1906, the diameter of the organ in the cat may under these circumstances be only 1.5 or 2 cm. — a smallness of size almost incredible.²⁶

Whether the extrinsic nerves are present or not, therefore, the muscles of the gastric wall must be in tonus, and must be placed in tension by the contents before response will occur. In all probability the vagi normally adapt the size of the organ to the varying amount of food taken in. Thus, if the stomach were relaxed, these nerves might set the muscles in tension about a small amount of food which otherwise would not produce any tension whatever. If these nerves are severed, however, the intrinsic tonus which appears, compensates by rendering the stomach so contracted that, even if only a small amount is swallowed, the muscles are stretched, and peristaltic activities are at once started.

The question now arises as to the stage in the digestive process at which the vagus influences affect gastric tonus. I have previously stated that the severance of the vagi shortly before the ingestion of food is followed by inactivity for a considerable period. After digestion is well started, however, I have found, both by X-ray observations, and by inspection and records of intragastric pressure when the digesting stomach was exposed under warm salt solution, that the vagi can be severed without altering either the character of gastric peristalsis or the rate at which the stomach empties. The condition for peristaltic activity seems to be given to the stomach when the food is taken, and after that the stomach appears able to maintain that condition by itself.

That during the mastication and ingestion of food impulses pass down the vagi to the stomach, was proved by Pawlow's observations on the psychic secretion of gastric juice.²⁷ As already stated, repeated stimulation of the vagi results in an increased tonic state, which is much more persistent than that following a single stimulation. Since a tonic state is necessary for gastric peristalsis, and since peristalsis does not appear if the vagi are cut shortly before the ingestion of food, the inference is suggested that, just as there is psychic secretion, so likewise there is psychic tonus, aroused while food is being ingested.

²⁶ CANNON: This journal, 1906, xvii, p. 432.

²⁷ PAWLOW: The work of the digestive glands, London, 1902, p. 50.

How gastric tonus, once established at the beginning of digestion, is maintained thereafter though the vagi be cut, is not yet determined. The presence of hydrochloric acid in the stomach, according to Edelmänn, is the requisite stimulus for peristalsis.²⁸ Ducceschi had earlier noted that the acid applied to the cardiac end augmented the contractions,²⁹ and Hedblom and I observed that feeding acid food was attended by especially deep and rapid peristaltic waves.³⁰ Though there is this evidence of the concomitance of acid gastric contents and peristalsis, the conclusion that the relation is essential is not well supported. The empty stomach of a fasting animal is often found in tonic contraction and exhibits peristalsis as soon as distended, before acid secretion occurs; and powerful peristaltic waves may occur when the gastric contents are strongly alkaline.³¹ Tonus, as a basis of peristalsis, is not, therefore, dependent on acid gastric contents.

The carbon dioxide content of the blood has been invoked by Henderson as the stimulus for peristalsis.³² That increasing carbon dioxide in the blood is attended by increased tonus is easy to demonstrate. I have seen intragastric pressure rise from between 1 and 2 cm. of water to between 8.5 and 10 cm., and peristalsis change simultaneously from shallow to deep waves, as a result of adding a 40 cm. rubber tube to the tracheal cannula. Although the digestion of a meal is accompanied by an increase in the respiratory exchange, the carbon dioxide content of the blood during this time is probably not sufficiently different from its content at other times to account for the persistent tonus. Indeed the fasting stomach, as previously stated, may be found in strong tonic contraction.

Possibly the slow decrease in size (increase in tonic contraction) of the stomach, as the muscle contracts rhythmically, results from the "contraction remainder" of smooth muscle. This phenomenon, to which Schultz called special attention,³³ consists in the failure of

²⁸ EDELMANN: Dissertation (Russian) abstracted in the *Jahresbericht über die Fortschritte der Physiologie*, 1906, xv, p. 119.

²⁹ DUCCESCHI: *Archivio per le scienze mediche*, 1897, xxi, p. 154.

³⁰ HEDBLOM and CANNON: *American journal of the medical sciences*, 1909, cxxxviii, p. 518.

³¹ CANNON: *This journal*, 1907, xx, p. 299.

³² HENDERSON: *This journal*, 1909, xxiv, p. 71.

³³ SCHULTZ: *Archiv für Physiologie*, 1903, Supplement-Band, p. 124 also BIEDERMANN: *Archiv für die gesamte Physiologie*, 1904, cii, p. 520.

the muscle to relax fully before the occurrence of another contraction. Evidently, if such a remainder were left as a heritage to each successive shortening, a process of adding would occur. The muscles would become more and more contracted — *i. e.*, the circumference of the stomach would be slowly diminished. The step-like rise in the pressure curve (Fig. 1) is explicable on the basis of the tonic state being built up of single contractions, the relaxation phases of which are not complete. Such a process can be observed in the excised stomach. I have tied the digesting stomach at the two ends, removed it from the body, placed it in warm oxygenated Ringer's solution containing 0.5 per cent barium chloride, introduced a glass tube which rose above the gastric level, and observed for nearly a half-hour peristaltic waves passing over the organ and the contents being gradually discharged as the capacity diminished. About 125 c.c. of material was thus gradually discharged. The stomach, therefore, seems to grow smaller by its own rhythmic contractions.

If a "contraction remainder" is to account for the gradual increase of the tonic state as digestion proceeds, it must act differently at different parts of the stomach. The mid-portion grows smaller much faster than the antrum (see Fig. 3). The process of adding to the contracted state must be therefore rapid and marked in the mid-portion, and only slight in the antrum. This differential effect is possibly accounted for by Ducceschi's observation that hydrochloric acid introduced into the antrum causes a diminution of the contractions in that region.³⁴ Thus the stronger musculature of the antrum would be held in check, while the rest of the stomach grew steadily smaller. The whole question of increasing tonus, however, must wait for further information regarding the nature of the tonic state in smooth muscle.

SUMMARY AND CONCLUSIONS.

Gastric peristalsis is like colonic antiperistalsis in consisting of serial waves starting at a pulsatile source and advancing without far-projected inhibition. Nicotine does not stop them.

Gastric peristalsis results from tension produced by internal pressure acting on the tonically shortened gastric musculature, — for (1)

³⁴ DUCCESCHI: Archivio per le scienze mediche, 1897, xxi, p. 154.

distention of the inactive stomach causes peristalsis when the musculature is tonically shortened, but not when it is relaxed; (2) considerable intragastric pressure (sustained tension) prevails in the stomach manifesting peristalsis; and (3) within limits peristalsis is augmented or weakened as intragastric pressure is experimentally increased or decreased. Tension can be produced by stretching tonically contracted muscle walls with increased contents, or by inducing tonus in the muscle.

The pulsatile source of the gastric waves has no fixed seat. The conical shape of the stomach permits a graded relation between internal pressure and the tonic musculature. The region that pulsates is that which is not over-distended or inadequately distended. By increasing internal pressure the over-distended region at the cardiac end is enlarged, and the source of the waves is moved towards the pylorus where the muscles have greater mechanical advantage.

The pulsations of the circumference where the waves start can be explained as the result of pressure causing contraction, and thus relative refractoriness to stimulation until relaxation is occurring. Then the ring is again stimulated as before.

The passage of peristaltic waves away from the source can be explained as the result of increased internal pressure,—for (1) increased internal pressure brings parts towards the pylorus into activity (see above); (2) internal pressure is greater as the pylorus is approached; and (3) the waves can move smoothly from the source to the pylorus when the continuity of the myenteric plexus is interrupted by many incisions encircling the stomach.

As the stomach empties, the cardiac incisure becomes the most contracted place. As such it pulsates most readily, and starts the peristaltic waves. Only when the medium for distributing internal pressure — *i. e.*, the contents — disappears, does peristalsis normally cease.

Tonus as an essential factor of gastric peristalsis is first given by vagus impulses and later maintained by the stomach itself,—for (1) severing the vagi before feeding results in inactivity, (2) severing the vagi after digestion is started causes no change in gastric movements or in the rate of discharge. Probably a psychic tonus is developed by the taking of food. The method of maintaining the tonic state locally as digestion proceeds, and of increasing it as the stomach

empties, is not yet determined; it may be the result of a "contraction remainder" after each rhythmic pulsation.

The above results account for the functions of the vagi and the splanchnics. They are nerves which increase or decrease the tonus of gastric musculature, and thereby affect peristalsis. The absence of stomach movements, for example, in states of exhaustion, can be explained by the failure of vagus impulses; and in emotional states, by the presence of splanchnic impulses. Both conditions result in absence of gastric tonus.

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